

HELPERS AT THE NEST IN THE WHITE-FRONTED BEE-EATER

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Cooperative reproduction in birds is a rare but somewhat predictable phenomenon. Roughly 80 species (about 1 per cent. of all bird species) including 52 African species representing 30 families or sub-families (Grimes 1976) are known to have regular helpers. About 20 of these have been studied in detail, and these studies have indicated several trends. Cooperative species tend to be tropical or sub-tropical in distribution, sedentary (and often highly territorial), and live in somewhat arid areas. Often helpers (often called auxiliaries) are young birds from previous generations who are helping their parents, but there are many other types of social systems (for reviews see Brown 1974, Woolfenden 1976 and Emlen 1978). One group of birds in which cooperative breeding is relatively well developed is the family Meropidae, the bee-eaters.

Seventeen of the 24 species of bee-eaters live in Africa some living in forest areas, some living in savanna. Forest species tend to be solitary, savanna species tend to be colonial. Many of the savanna-dwelling bee-eaters exhibit a high degree of cooperative breeding, while at the same time being highly colonial (Fry 1972a, Emlen 1978 and in press). Most of the well studied cooperative species have a social structure where individuals roost, breed, and forage throughout the year on a single all-purpose territory. White-fronted Bee-eaters on the other hand, roost and breed colonially and disperse daily to forage, often travelling several kilometres from the colony. Bee-eaters, then, offer an opportunity to investigate the theories of cooperative breeding in an ecological context different from that of most other cooperative species.

This paper is a preliminary report of part of an on-going study of the White-fronted Bee-eater *Merops bullockoides* in the Lake Nakuru National Park, Kenya. *Merops bullockoides* is locally common throughout most of central Africa, ranging from the Zambezi River north through East Africa to central Kenya. In Kenya it is locally common in the Rift Valley. Our study site is located in an area of mixed grassland and bush punctuated with patches of riverine woodland lining the two seasonal rivers that flow into Lake Nakuru from the south. It is along these two rivers that the birds find suitable nesting areas.

Merops bullockoides is highly colonial and roosts and breeds in holes in vertical sandbanks along rivers and in other suitable areas. Breeding colonies range in size from 20 to 150 active holes, most being between 25 and 50. Breeding can occur in nearly every month, but most colonies breed between October and June. Even when not breeding, the birds remain gregarious and roost in the colonies.

White-fronted Bee-eaters feed primarily on flying insects which they capture by 'flycatching', but they also swoop down and pick insects from grass or the surface of water. Venomous Hymenoptera make up a significant portion of the diet, but they seem to take a relatively high proportion of Lepidoptera, Diptera and Orthoptera as well. Nestlings are rarely fed venomous insects. For a more general review of bee-eater biology, the reader is referred to Fry (1972b).

In Kenya, *M. bullockoides* exhibits a high degree of cooperative breeding. In addition to breeding together, members of a group (parents plus helpers) roost together and forage together throughout the year. During

breeding, helpers, which are of both sexes, assist in cleaning out old holes, incubation, feeding nestlings, and escorting and feeding fledglings. In 1977 and early 1978, the mean group size was 2.7 individuals and 49 per cent of all nests had at least one helper. Most helpers appear to be young birds who are assisting their parents in the rearing of later broods.

The major focus of our study is to understand why bee-eaters cooperate reproductively. In other words, what advantages do parents and helpers accrue from this cooperation? Current theories postulate two general types of advantages: direct advantages in breeding or survival, and indirect benefits through kin selection and inclusive fitness. Parents may gain increased breeding success or efficiency; helpers may gain valuable breeding experience before they initiate breeding on their own; and both may gain increased foraging efficiency or predator detection and protection by living together in a group. Indirectly, all may gain increased inclusive fitness via kin selection if helpers tend to assist individuals to whom they are related. For a more thorough discussion of these theories, see Alexander (1974), Wilson (1975), Emlen (1978) and Brown (in press).

In any study of cooperative birds, it is essential to be able to identify individuals and to follow these birds continuously for several years through successive breeding attempts. We capture the bee-eaters by putting mist nets in front of their colony at night; they are permanently marked by E.A.N.H.S. numbered rings. To identify individuals without having to recapture them, we use a coloured plastic wing-tag, called a 'saflag' that is wrapped around the humerus. Symbols of various design and colour are painted on the saflags, which also occur in several colours, and permutations of these enable us to identify several hundred birds individually.

Observations are concentrated at breeding or roosting colonies, using observation hides, during the two or three hours prior to sunset. At this time the birds go through a period of intense social activity, and it is possible to record which birds roost together and other relevant behavioural data. During breeding, these observations are supplemented by early morning counts of the birds emerging from holes (to determine group sizes) and counts of feeding visits during the mornings and afternoons. Breeding holes are inspected three times a week using a special periscope (Demong & Emlen 1975), and with this instrument it is possible to accurately determine clutch-size, hatch dates, and the number and ages of nestlings. Just prior to fledging, the young are carefully removed from the nest, weighed, measured, ringed, saflagged, and returned to the nest.

As this paper is a preliminary report of an on-going research project we will discuss only some aspects of reproduction which are relevant to an understanding of the adaptive significance of cooperative breeding. Overall breeding success in *M. bullockoides* has been low in recent years. Large scale breeding occurred during the long rains of 1977 and 1978, but only 16 per cent of all eggs laid during these seasons produced viable fledglings. Thirty-four per cent of these failures were the result of two disastrous floods on the Makalia River, each destroying all or nearly all holes in a breeding colony. Of the remaining failures, 31 per cent were caused by starvation, as evidenced by a retarded development and the slow disappearance of one, two, or more young from each nest. Even among the successful nests (here defined as those successfully fledging at least one young), reproductive success (RS), the proportion of eggs that produce a fledgling, was fairly low. In the vast majority of holes,

at least one fledgling died, and only 14 per cent of all successful groups had 100 per cent RS. This suggests that, at least in these years, bee-eaters had difficulty in obtaining sufficient food to feed their nestlings.

TABLE 1

Comparison of reproductive output of White-fronted Bee-eaters breeding as pairs or as groups with helpers. Data are from six colonies that bred during the long rains of 1977 or 1978

	No. of Nests	Average Clutch	Average No. of fledglings produced	Reproductive success	Average feeding rate (visits to young/hour)
Pairs alone	50	2.54	0.60	21%	5.1 (data from 21 nests)
Pairs + helpers	31	3.06	1.26	40%	6.6 (data from 17 nests)

If food is limiting, it seems reasonable to try to relate breeding success to group size and to the amount of food each group brings to the nest. This is done in Table 1, using data from six colonies which bred during the long rains of 1977 and 1978. Only holes in which all relevant parameters are known were used in this analysis. Nests that were lost due to chance catastrophic effects (flooding), where group size could play no role in influencing success, have been omitted from the analysis.

Although mean clutch sizes were not significantly different ($P > 0.05$, F-test), pairs with helpers had a much higher (40 per cent) reproductive success than pairs alone (21 per cent), and produced on average twice as many young per nest. Thus on a per group basis, pairs with helpers out-reproduced those without ($P < 0.05$, F-test). On a per pair basis, the average fecundity of birds in pairs was slightly higher than that of birds in groups. Thus while helpers increased the reproductive output of a group, this increase was not as great as one would expect from the simple addition of extra birds.

If food is limiting during breeding, then RS should be correlated with the amount of food brought to the nest. In other words, pairs with helpers should bring more food (or should bring food at a higher rate) than pairs alone. In February and May of 1978, feeding rates were recorded at two breeding colonies. Feeding visits were recorded for 24 h periods in the morning and afternoon on two successive days (for a total of 10 observation hours per nest) when the nests contained young of between 5 and 10 days of age. Bee-eaters bring one food item per feeding trip, and although the size of the item brought varies considerably, simple analysis of the number of visits can be useful. Mean feeding rates for young being tended by pairs and groups are listed in the last column of Table 1. Pairs with helpers brought on average 29 per cent more food per hour than pairs alone, a result which correlates with their observed increase in RS. It thus appears that helpers do in fact contribute to increased breeding success, and one major way in which this is done is by increasing the amount of food brought to the young.

The results thus far describe advantages only to the parents, not the helpers. Why, then, should helpers 'help' instead of breeding on their

own. Unfortunately it takes many years of observation to answer that question, and our study has not yet progressed far enough to do so. At this point we can only list the types of data we wish to collect in order to understand the advantages to helpers. If helpers gain valuable breeding experience by helping for one or two years before they initiate breeding themselves, then one expects the breeding success of the *initial* attempt to be higher in birds that have been helpers than in birds that have not. If kin selection plays a role, then helpers should selectively help their kin, and might even provide assistance to others in proportion to their degrees of genetic relationship. If helpers gained protection from predators or access to better feeding areas by virtue of group membership, then individuals that are members of groups should show a higher survival rate than individuals who are not.

To test these ideas, it will be necessary to continue to follow the same individual bee-eaters for several years, building up information on their genetic relationships, keeping track of the amount of assistance they provide to one another. With the continued cooperation of the National Museums of Kenya, the Ministry of Tourism and Wildlife, and the personnel at Lake Nakuru National Park, we hope to continue our study until such answers are obtained.

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